

Patch Formation by the Ectoparasitic Snail *Boonea impressa* on Its Oyster Host, *Crassostrea virginica*

by

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Abstract. *Boonea impressa* (= *Odostomia impressa*) is a common ectoparasite of the oyster *Crassostrea virginica*. Snail populations are contagiously distributed. Studies were conducted to determine what factors influence patch formation of *B. impressa* in oyster populations. Physical characteristics of oysters such as orientation, age, size, and level of *Perkinsus marinus* (= *Dermocystidium marinum*) infection did not affect host acceptability in adult snails. Patch formation occurred independently of any tested oyster characteristic. Aggregates usually formed on the clumps nearest where snails were initially placed. Snails moved frequently from host to host, but snails preferentially moved between existing aggregates. Although up to 35% of the population moved daily, patch location remained stable for at least 5 to 6 days. Patches may form through chance meetings during foraging and grow in size as a result of gregarious behavior. Patches were spatially more stable than the individuals that composed them indicating that refugia from snail parasitism may exist in oyster populations. Therefore, the effect of this parasite on its host population may depend more on the spatial and temporal dynamics of the patch than on the parasites themselves.

INTRODUCTION

Movement and patch formation of gastropod populations occur on different temporal and spatial scales depending on the reason for aggregation. Patches form for reproduction, feeding (FEARE, 1971; CATTERALL & POINER, 1983), and protection from physical conditions (HAZLETT, 1984; GARRITY & LEVINGS, 1984), for example. Factors influencing gastropod behavior include season (FEARE, 1971), maintenance of position in the intertidal zone (HAZLETT, 1984), diurnal rhythms, and chemotaxis (RHODE & SANDLAND, 1975). In some cases, factors initiating the

aggregation disappear long before the aggregate does (HARTNOLL & HAWKINS, 1985).

The pyramidellid gastropod *Boonea impressa* (= *Odostomia impressa*) is a mobile ectoparasite with an aggregated distribution on its host, the American oyster, *Crassostrea virginica* (POWELL *et al.*, 1987). *Boonea impressa* is numerically abundant in oyster reef communities with numbers reported as high as 100 per oyster (HOPKINS, 1956). Five to 40 snails per oyster occur frequently in Texas bays (WHITE *et al.*, 1984). Although common, information on behavior in pyramidellids is generally lacking. The pyramidellids are considered entirely parasitic, and anatomical data, although rare, support this conclusion (FRETTER & GRAHAM, 1949; FRETTER, 1951). *Boonea impressa* feeds much like a mosquito by piercing the host with a hollow

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stylet and sucking the body fluids with a buccal pump (FRETTER & GRAHAM, 1949; FRETTER, 1951; ALLEN, 1958). *Crassostrea virginica* is the preferred host of *B. impressa* but, like other odostomians, it is not entirely host specific (ROBERTSON & ORR, 1961; BULLOCK & BOSS, 1971).

Parasitism by *Boonea impressa* alters the growth, reproduction, and metabolic condition of its host (WARD & LANGDON, 1986; WHITE *et al.*, in press). *Boonea impressa* can transmit an important disease-producing parasite, *Perkinsus marinus* (= *Dermocystidium marinum*) from host to host (WHITE *et al.*, 1987) and increase infection intensity in previously infected hosts. Therefore, *B. impressa* may have an important, detrimental effect on oyster health, community structure, and population dynamics.

Shape, texture, size, age, movement, and chemical substances all influence host selection in parasites (VINSON, 1976). If the host is distributed patchily, parasites may concentrate their search on patches of higher host density or remain in patches for longer periods of time searching for a suitable host (HASSELL, 1982a; WAAGE, 1983; CHANTARASA-ARD *et al.*, 1984). Under certain circumstances, host populations can thereby be regulated (*e.g.*, HUFFAKER *et al.*, 1986; CHESSON & MURDOCH, 1986). The distribution of the effect of snail parasitism on oyster populations is determined by the location and temporal stability of snail patches. Snails are consistently more patchily distributed than their hosts, but the spatial position of snail patches is not uniformly correlated with that of their hosts. Hence the distribution pattern is best described as host-density vague (POWELL *et al.*, 1987). POWELL *et al.* (1987) suggested that most oysters are acceptable hosts so that factors inherent to the host and its distribution have little effect on snail distribution. Snail patches were considered to form randomly, possibly as foraging-time aggregates, and be maintained by a behavioral change to gregariousness, as is frequently the case in insect swarming behavior (OKUBO, 1980).

Whether patches are random occurrences or not and to what degree patches are temporally stable determine the nature of refugia from parasitism in oyster populations and the resulting effect of parasites on the stability of the host population. The purpose of this study was to determine whether characteristics of the oyster population influence patch formation and location in populations of *Boonea impressa* or whether patches form randomly. Oyster characteristics investigated included position, orientation, age, and the presence and infection intensity of *Perkinsus marinus*. That is, we asked the questions, are some oysters more acceptable hosts than others and does differential acceptability affect patch location?

MATERIALS AND METHODS

All snails and oysters used in the studies were collected from reefs in the Copano Bay-Aransas Bay area of the Texas coast (figs. 1 and 2 in POWELL *et al.*, 1987). Experiments were conducted during the summers of 1984

and 1985 at the University of Texas Marine Science Institute at Port Aransas, Texas.

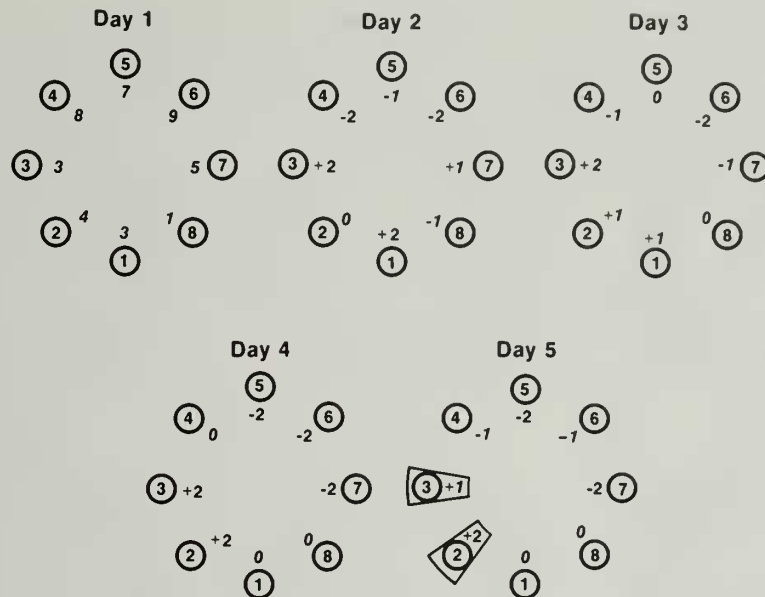
To study patch formation, oysters were arrayed in a circle in trays completely submerged on a flowing sea table. Seawater supplying the sea table was piped directly from Aransas Pass via an intermediate settling chamber to remove larger particulates. The seawater source and drain were upstream and downstream of the tray, respectively, so that seawater flowed unidirectionally across the tray during the experiment. Seawater temperature was 20–22°C. Aeration was unnecessary.

To initiate an experiment, individuals of *Boonea impressa* were added to the center of the circle of oysters. Consequently, all snails were initially equidistant from all oysters. The number of snails on each oyster was counted daily, and the oysters replaced in the same position in the circle. Four preference tests were conducted, examples of which are depicted in Figures 1–7.

(1) Snail preference for hosts in different spatial orientations was tested by placing 12 oysters alternately horizontally (left valve down) and vertically (dorsal edge down) in the circular arrangement depicted in Figure 6. The number of snails on each oyster was recorded daily for 5 days.

(2) Eight adults (5–7 cm in length), eight juveniles (2–3 cm in length), and eight groups of spat (seven per group) were placed in a circular arrangement to ascertain snail preference for oysters of different age and size. Seven spat were used per group so that sufficient feeding space would be available to prevent snail crowding from interfering with patch formation. The number of snails on each oyster or group of spat was recorded daily for 6 days. The snails were then removed, the same oysters randomly rearranged around the circle (as shown in Figure 5), and the same snails placed again in the circle's center. Snail position was recorded for another 4 days.

(3) Snail preferences might involve more subtle cues than host orientation or size. To determine whether patches formed on preferred oysters for any reason or on oysters placed in preferred positions in the circle, adult oysters of approximately equal size were used. Snails were allowed to form patches over a period of days. The snails were then removed and the same oysters rearranged in the circle. The same snails were added a second time and their position recorded each subsequent day. Either preferred oysters or preferred positions could then be identified and further analyzed. Two replicate experiments were run. In the first, eight oysters were arranged in a circle. Snail position was recorded daily for 5 days, the oysters rearranged about the circumference, the same snails added to the center, and their position monitored daily for 5 more days. Finally, the oysters were rearranged a third time, the same snails added again, and their positions monitored again for 5 days. The three different arrangements are shown in Figure 2. In the second experiment, 19 oysters were arranged as shown in Figures 3 and 4. Snail positions were monitored twice daily for 6 days, the oysters randomly rearranged, the same snails again added to the circle's



Adult Choice Experiment

Figure 1

Representative results of snail patch formation on adult oysters. Numbers within circles designate individual oysters (No. 1, No. 2, etc.). Numbers outside circles designate the net number of snails added or lost by that oyster over the previous 24 h, except for day 1 which shows the initial distribution. Rectangled oysters (day 5) indicate location of final aggregates (see Figure 2).

center, and the snail's positions recorded twice daily for another 6 days.

(4) To determine whether snails preferred nearby oysters, 20 oysters were placed randomly on a flooded sea table as shown in Figure 7, and snails added to the center. The number of snails on each oyster was counted once a day for one week.

After the experiments were concluded, each oyster was assayed for the presence and intensity of infection by *Perkinsus marinus* by excising a small piece of mantle tissue and culturing it in thioglycolate medium (RAY, 1966).

Infection was determined microscopically after staining with Lugol's solution and the intensity of infection was scored using the semiquantitative 0-to-5-point scale of MACKIN (1962).

RESULTS

Representative distributions of snails among oysters are depicted in Figures 1–7. A minimum estimate of the number of snails moving daily can be made by summing the number of snails lost by oysters having fewer snails at the

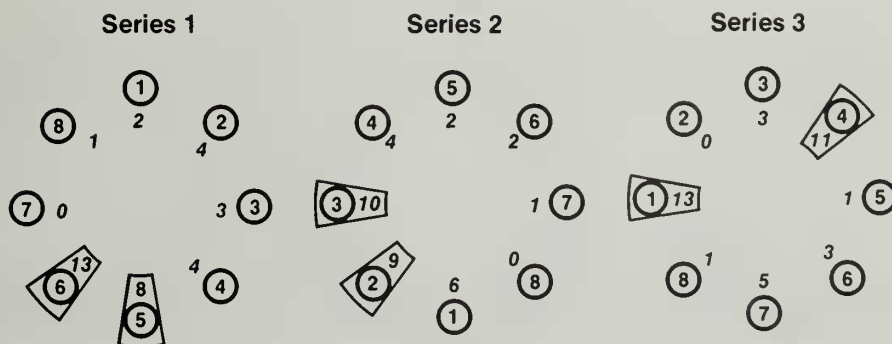


Figure 2

Patch formation of snails on the same adult oysters occupying different positions in the circle (see also Figure 1). The circled numbers designate individual oysters, and the uncircled numbers the number of snails at the end of each series, at which time all snails were removed and all oysters repositioned as described in the Methods Section. Rectangled circles indicate locations of aggregates.

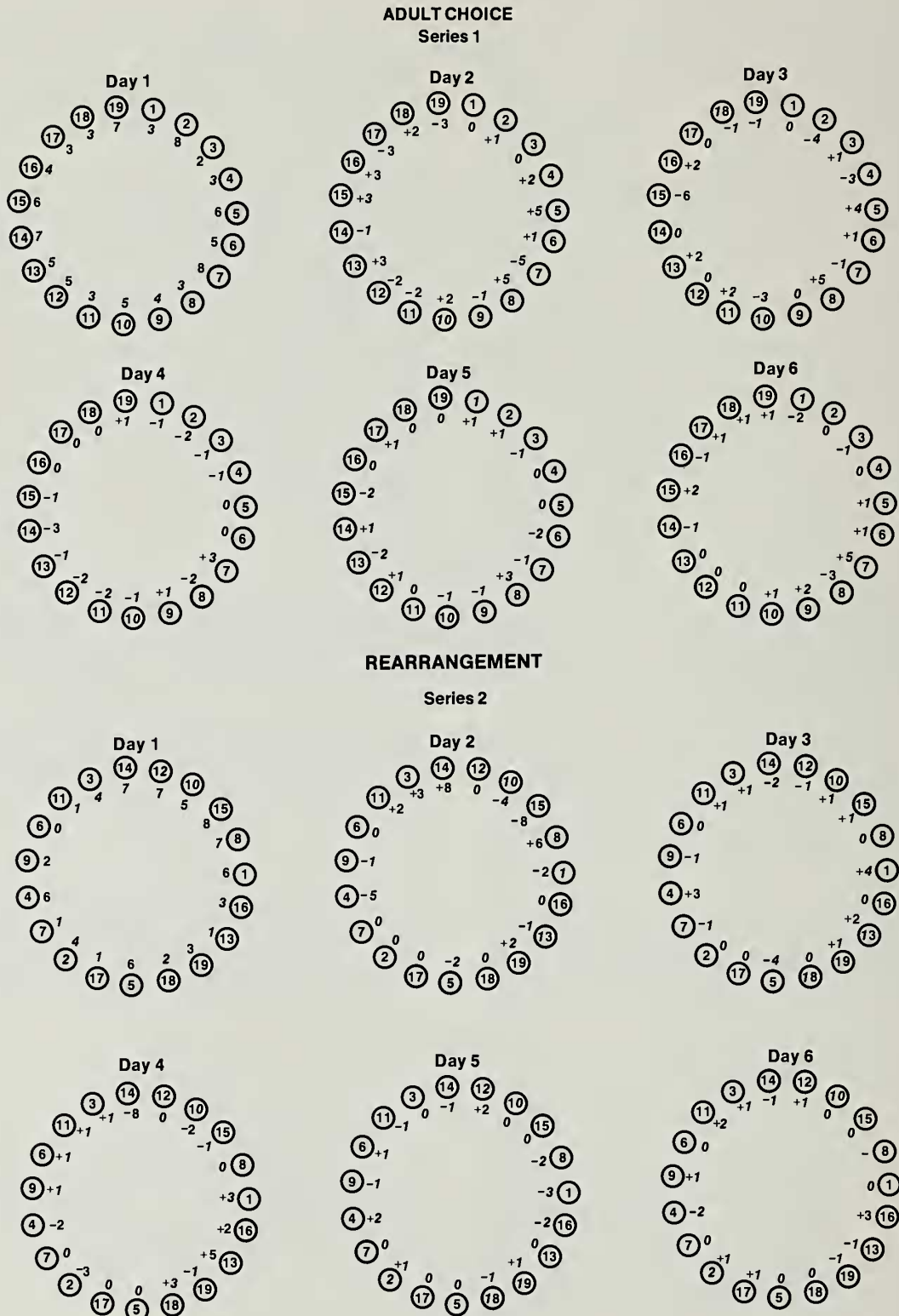


Figure 3

Representative results of snail patch formation on adult oysters (see also Figure 4). Numbers within circles designate individual oysters (No. 1, No. 2, etc.). Numbers outside circles designate the net number of snails added or lost by that oyster over the previous 12 h, except for day 1 which shows the initial distribution.

next daily observation. At least 10–20% of the snails moved each day in experiments where oysters were arranged in a circle. In the experiment where oysters were arranged randomly on the sea table, at least 20–35% of the snails moved each day.

Differences in snail distribution from one observation to the next were assessed by Spearman's rank analysis (Tables 1–5). A significant difference using this test indicates that the two distributions compared were similar to each other. Typically, the longer the experiment went on, the more the initial distribution varied from the final distribution. Usually distributions separated by 3 or more days were no longer similar enough to produce a significant correlation. The significance of contagious (patchy), random, and even distributions were judged using chi-square tests ($\alpha = 0.05$) of I , where $I = s^2/\bar{x}$, as described by ELLIOTT (1977). In all experiments, the snails' final distribution was contagious (Table 6). Snail distribution was frequently random during the initial few days of observation, however. Hence, the distributional pattern became more contagious as the experiment progressed. In general, oysters that had snail aggregates continued to recruit snails from other oysters initially and then maintained a larger number despite continued snail relocation. That is, the number of snails moving daily did not obviously decrease with time during most experiments. Moreover, in most experiments, we used an average of 4 to 6 snails per oyster; yet the maximum number observed on any oyster was only 17. Hence, on the average, snails tended to relocate by moving to and from existing aggregates once the aggregates became established and, after a time, aggregates ceased to grow in size.

To determine whether the location of snail aggregates was really temporally stable or not, we tabulated, for each oyster, the number of observations in which its number of snails was above or below the daily mean for all oysters. If the location of snail aggregates was temporally stable, then the number of times the oyster was observed to be above or below the daily mean should differ significantly from a 50:50 split using the binomial test. The oyster would tend to remain above or below the mean from one observation period to the next. By chance, some oysters may produce significant results. Hence, the number of significant results was itself tested for significance using the same test. Aggregates were judged temporally stable in an experiment when the number of oysters in the experiment that differed significantly from a 50:50 ratio (number of observations above the daily mean : number of observations below the daily mean) was more than would be expected by chance at $\alpha = 0.05$. The results were significant in all cases. In fact, most oysters having less or more snails than the mean on the second day retained that relative position with respect to the mean throughout the remainder of the experiment.

Intensity of infection by *Perkinsus marinus* ranged from uninfected to heavily infected (0 to 5 on Mackin's 1962 scale). With one exception, infection intensity did not sig-

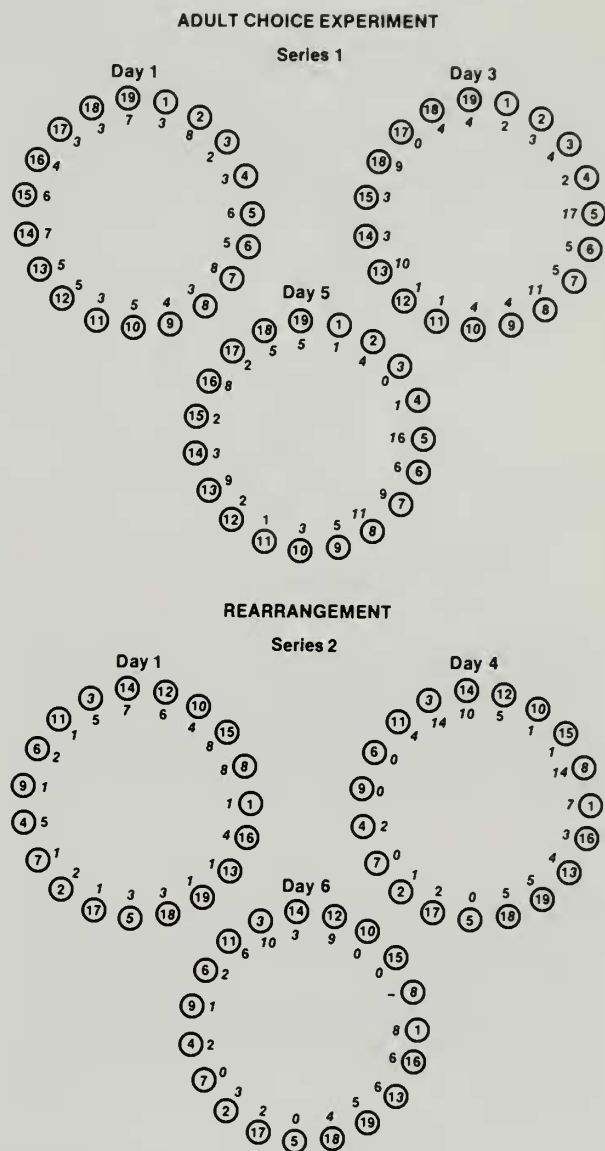


Figure 4

Patch formation of snails on adult oysters occupying different positions in the circle (see also Figure 3). The circled numbers designate individual oysters, and the uncircled numbers the number of snails at the end of each series, at which time all snails were removed and all oysters repositioned as described in the Methods Section.

nificantly correlate with snail distribution on oysters, however (Tables 1–5) (Spearman's rank, $\alpha = 0.05$). There was no significant difference in the number of snails on vertically or horizontally oriented oysters (Table 1, Figure 6) (Mann-Whitney, $\alpha = 0.05$) or on adults, juveniles, or groups of spat (Table 3, Figure 5) (Duncan's multiple range on ranked data, $\alpha = 0.05$).

In the experiments where the same oysters were rearranged into different positions around the circle, the final

SPAT/JUVENILE/ADULT CHOICE EXPERIMENT

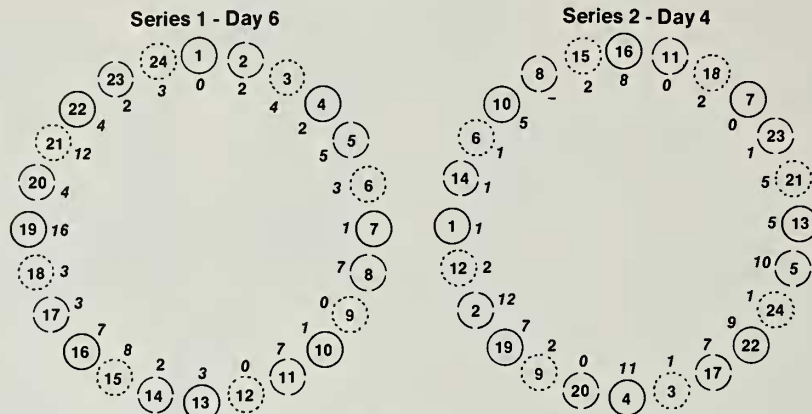


Figure 5

Results of the experiment using oyster adults, juveniles, and groups of spat. Figure layout as in Figure 2. Solid circles, adults; dashed circles, juveniles; dotted circles, spat.

distribution of one series was never correlated with the final distribution of the other (Figures 2, 4, 5) (Spearman's rank, $\alpha = 0.05$). Snails formed aggregates on particular oysters in the first series, and when the oysters were repositioned in the circle, the snails formed aggregates again, but not necessarily on the same oysters.

Moreover, snails were not attracted preferentially to any set of positions on the circle's circumference. In all three experiments where oysters were repositioned, the distribution of snails at the end of the succeeding trial was not significantly correlated with respect to position in the circle with the distribution at the end of the preceding trial (Figures 2, 4, 5) (Spearman's rank, $\alpha = 0.05$). Hence, snail distribution resulted from intrinsic snail behavior rather than from environmental stimuli or differential host acceptability.

In the experiment where adults, juveniles, and groups of spat were used, the distribution of snails within any one of these three categories in the first series was not significantly correlated with the same distribution in the second (Figure 5). Hence, the observation that aggregates did not form consistently on any particular set of oysters held also for specific size classes.

In one experiment, oysters were distributed on a sea table so that some were farther from the position where snails were added than others (Figure 7). Aggregates formed preferentially on oysters near the position where snails were added even though snails could and did move to the farthest oyster by the end of the first day. These aggregates remained stable throughout the rest of the experiment even though 30% or more of the snails changed positions each day.

ORIENTATION EXPERIMENT

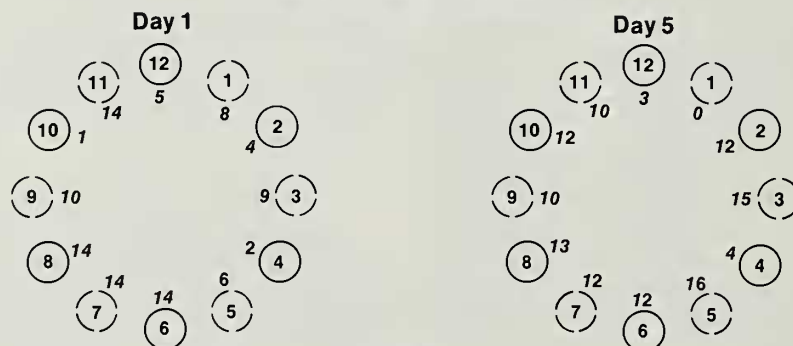


Figure 6

Results of the oyster orientation experiment showing snail positions on first and last day of one experimental series. Figure layout as in Figure 2. Solid circles, horizontal (left valve down) oysters; dashed circles, vertical (dorsal edge down) oysters.

TABLE EXPERIMENT

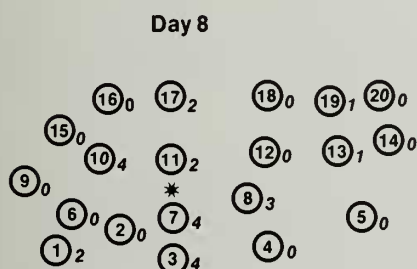
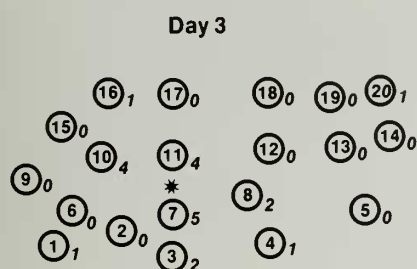


Figure 7

Results of experiment with oysters positioned at various distances from the location (*) where snails were added. Snail positions on days 3 and 8 of the experiment are shown. Figure layout similar to Figure 2. Distance from * to oyster No. 7 is 9 cm.

DISCUSSION

The distribution of parasites on their hosts is an important factor determining the impact of the parasite on the host population (HASSELL, 1982a; ANDERSON & GORDON, 1982). The location of parasite patches can be influenced by a wide variety of factors including host size, shape, and spatial distribution, and the presence of gregarious behavior or interference competition among the parasites (VINSON,

Table 1

Results of Spearman's rank correlations for snail distributions in the experiment using vertically and horizontally positioned oysters (Figure 6). SC, correlation significant (distributions similar) at $\alpha = 0.05$. Analysis of *Perkinsus* used data on disease intensity for the last day of the experiment only.

Day	Day				
	1	2	3	4	5
1	—				
2	X	—			
3	X	SC	—		
4	X	X	X	—	
5	X	X	X	SC	—
<i>Perkinsus</i>	X	SC	SC	X	X

Table 2

Results of Spearman's rank correlations for snail distributions in the experiment with oysters positioned at various distances from the location where snails were initially added (Figure 7). See Table 1 for further explanation.

Day	Day							
	1	2	3	4	5	6	7	8
1	—							
2	SC	—						
3	X	SC	—					
4	SC	SC	SC	—				
5	X	SC	SC	SC	—			
6	X	SC	SC	SC	SC	—		
7	X	SC	SC	SC	SC	SC	—	
8	X	SC	SC	SC	SC	SC	SC	—
<i>Perkinsus</i>	X	X	X	X	X	X	X	X

1976; NAGEL & CADE, 1983; WEIS, 1983). *Boonea impressa* did not prefer to aggregate on oysters of a particular size, spatial orientation, or level of infection by *Perkinsus marinus*. Nor were any other intrinsic characteristics of the oysters important in determining snail distribution. In all cases where oysters were used in more than one experimental series, *B. impressa* did not consistently select the same suite of oysters for patch formation. POWELL *et al.*

Table 3

Results of Spearman's rank correlations for snail distributions where oyster adults, juveniles, and groups of spat were used (Figure 5). SC, correlation significant at $\alpha = 0.05$. Analysis of *Perkinsus* used data on disease intensity for the last day of the last series only.

Series 1

Day	Day				
	1	2	3	4	5
1	—				
2	SC	—			
3	SC	SC	—		
4	SC	SC	SC	—	
5	X	SC	SC	SC	—
<i>Perkinsus</i>	X	X	X	X	—

Series 2

Day	Day					
	1	2	3	4	5	6
1	—					
2	SC	—				
3	SC	SC	—			
4	SC	SC	SC	—		
5	SC	SC	SC	SC	—	
6	SC	SC	SC	SC	SC	—
<i>Perkinsus</i>	X	X	X	X	X	X

Table 4

Results of Spearman's rank correlations for snail distributions in the experiment using only adult oysters (Figures 1-2). See Table 3 for further explanation.

Series 1					
Day	Day				
	1	2	3	4	5
1	—				
2	X	—			
3	X	SC	—		
4	X	SC	SC	—	
5	X	SC	SC	SC	—
<i>Perkinsus</i>	X	X	X	X	X

Series 2

Day	Day				
	1	2	3	4	5
1	—				
2	SC	—			
3	X	X	—		
4	X	X	SC	—	
5	X	X	X	SC	—
<i>Perkinsus</i>	X	X	X	X	X

Series 3

Day	Day				
	1	2	3	4	5
1	—				
2	SC	—			
3	SC	SC	—		
4	SC	SC	SC	—	
5	SC	SC	SC	SC	—
<i>Perkinsus</i>	SC	SC	X	SC	SC

(1987) suggested, from field data on snail distributional patterns, that acceptable oyster hosts must occur frequently in the population. Our data suggest that essentially all oysters are equally acceptable to adult snails. Juvenile snails, of course, are more host-size restricted (POWELL *et al.*, 1987), but these were not used in our experiments.

Initially, aggregates continued recruiting members over time, so that the snails' distribution gradually became more contagious. The number of snails was usually limited, however, to 10-15 snails per oyster. The same maximum densities are typically found in the field (WHITE *et al.*, 1984). When the distributional pattern became contagious, the frequency of snail movement did not decline. We observed that at least 10-20% of the snails moved per day throughout each experimental series. WHITE *et al.* (1984) estimated that, in the field, at least 50% of the snail population moved each week. Our data indicate that this is certainly an underestimate. WHITE *et al.* (1984) argued that physical dislodgment, by waves and currents for example, was an unlikely reason for snail relocation. Our

Table 5

Results of Spearman's rank correlations for snail distributions in the experiment using only adult oysters (Figures 3-4). See Table 3 for further explanation.

Series 1							
Day	Day						
	1	2	3	4	5	6	7
1	—						
2	SC	—					
3	X	SC	—				
4	X	SC	SC	—			
5	X	X	SC	SC	—		
6	X	X	X	SC	SC	—	
7	X	X	X	X	X	X	—
<i>Perkinsus</i>	X	X	X	X	X	X	X

Series 2

Day	Day			
	1	2	3	4
1	—			
2	SC	—		
3	SC	SC	—	
4	SC	SC	SC	—
<i>Perkinsus</i>	X	X	X	X

analysis supports this conclusion. Snails moved frequently even in the undisturbed environment of the laboratory.

Frequent snail movement, even after the snails' distribution became contagious, indicates that snails preferentially moved from one aggregate to another. RHODE & SANDLAND (1975), FEARE (1971), HAZLETT (1984), and GERHART (1986), among others, suggested that gastropods can locate other snails through the use of pheromones and mucus trails, thereby forming feeding or reproductive aggregates. Preferential movement between aggregates suggests that *Boonea impressa* may also be attracted by a chemical substance produced by other *B. impressa*.

The position of aggregates remained remarkably stable over periods of 5 days or so in spite of continual relocation by individual snails. FEARE (1971) documented a similar phenomenon for *Nucella lapillus*. POWELL *et al.* (1987) suggested that the locations where patches form might be a random process controlled by chance meetings of snails on oysters and that snails tended to move preferentially to nearby clumps so that aggregates tended to be near other aggregates. In the experiment where oysters were distributed at differing distances from the snail's original position, all aggregates occurred on the nearer clumps. More snails bestrode these clumps initially; snails had a greater chance to meet other snails on these clumps and aggregates formed.

The lengths of time a parasite searches for and remains on a suitable host are important determinants in the stability of parasite-host systems. Parasites may spend a large portion of their time searching for hosts that are distributed patchily in the environment (HASSELL, 1982b; MORRISON,

Table 6

I (ELLIOTT, 1977) for each day for each experiment. Asterisks indicate a significant contagious distribution ($\alpha = 0.05$). All other values were not significantly different from random.

Experiment	Day											
	1	2	3	4	5	6	7	8	9	10	11	12
Figure 2—Adults												
Series 1	0.78	0.51	0.32	1.89	3.95*							
Series 2	1.34	0.84	0.79	1.45	3.92*							
Series 3	0.59	1.57	1.75	2.22*	4.43*							
Figure 4—Adults												
Series 1	0.68	0.91	1.62*	2.36*	2.89*	3.41*	3.46*	3.94*	3.82*	3.14*	3.30*	
Series 2	1.75*	1.59	2.00*	4.41*	4.51*	4.13*	3.98*	3.60*	2.75*	2.98*	4.16*	2.62*
Figure 5—Adult, juvenile, spat	0.88	1.47	1.27	2.19*	3.87*	3.42*	2.03*	2.87*	3.04*	3.54*		
Figure 6—Orientation experiment	3.60*	1.75*	2.61*	2.19*	2.27*							
Figure 7—Distance experiment	1.73*	3.08*	2.23*	2.79*	3.41*	2.95*	3.19*	1.93*				

1986). POWELL *et al.* (1987) showed that *Boonea impressa* is more patchily distributed than its host on natural reefs. Optimal time allocation by the parasite would involve preferential searching in areas of high host density (WAAGE, 1983) because the efficiency of the parasite is partially determined by the time it takes moving between hosts (WEIS, 1983). Feeding cannot occur during this time. For *B. impressa*, reduced mobility once patches have formed would seem to maximize foraging efficiency. Curiously, *B. impressa* does not seem to minimize searching time but instead spends a large amount of time moving from aggregation to aggregation.

SUTHERLAND (1983) suggested that interference among parasites forces some to leave aggregations in search of areas of lower parasite density. Certainly physical feeding space is not limited at the densities we have observed. FORD (1986) demonstrated that continual bleeding of oysters could decrease hemolymph quality. However, as discussed earlier, there is no evidence that patches ceased to attract snails, nor did patches gradually disintegrate once formed. Hence, interference, directly as a result of decreased feeding space or indirectly by gradually reducing host acceptability as snail feeding continued, does not seem to offer a satisfactory explanation. WAAGE & DAVIES (1986) described a case in which host irritation increased at high parasite densities resulting in decreased parasite feeding efficiency. Oysters close their valves more frequently when snails feed (WARD & LANGDON, 1986), thus disrupting snail feeding. Perhaps this mechanism limits the size of snail patches by decreasing snail feeding efficiency and initiating emigration. SUTHERLAND (1983) lists a wide variety of other direct and indirect interference phenomena that might affect parasite or predator efficiency. Why *Boonea impressa* continually relocates from patch to patch remains an important question if we are to understand this snail's spatial distribution and its impact on oyster populations.

Despite the continual relocation of snails, patches retained their integrity for at least 4 to 5 days, the duration

of our experiments, without any sign of dissipating. Consequently, some oysters remain parasitized by many snails for periods of time long enough to affect scope for growth, fecundity, and disease incidence (*e.g.*, WHITE *et al.*, 1984, 1987, in press). The contagious distribution of *Boonea impressa* on oysters may be responsible for the patchy distribution of *Perkinsus marinus* on many reefs, for example. Moreover, some oysters in the population will be nearly snail free. Consequently, a refuge from snail parasitism exists, but the location is not predictable. Chance plays an important role in the distribution of patches. The extent to which refugia are a permanent feature depends upon the temporal stability of patches beyond the 5 to 6 day time period we used in these experiments. Regardless of their temporal stability, patches clearly are spatially more stable than the individuals that compose them. Hence, the effect of this parasite on its host population depends more upon the temporal and spatial dynamics of the patch than on the parasites themselves.

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